THE MORPHOLOGY, LIFE-HISTORY, AND SYSTEMATICS OF THE DIGENETIC TREMATODE, HOMALOMETRON PALLIDUM STAFFORD, 1904[1]

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Historical Background for the Investigation

The genus *Homalometron* was erected by Stafford (1904) to contain a new species, *H. pallidum,* from the intestine of *Fundulus heteroclitus.* There was no description or figure; instead, the new species was based on the description and figure by Linton (1901) of specimens collected from *F. heteroclitus* in the region of Woods Hole, Massachusetts. The species was not named by Linton whose account (p. 442) reads, "*Distomum* sp. (Pl. XXXII, Fig. 354) Aug. 7, 1899; 12. Aug. 28, 1899; 4. Intestine. Body very minutely spinose, white, translucent; acetabulum and oral sucker about same size; outline of body, long oval; neck short, continuous with body; greatest breadth in region of testes, near posterior end; ecaudate; acetabulum sessile; rami of intestines simple, elongate; esophagus as long as pharynx; testes, two, in median line behind uterus; seminal vesicle dorsal to ovary and posterior border of acetabulum; ovary between acetabulum and testes, on right side; pharynx, subglobular; genital aperture in front of acetabulum, on median line; vitelline glands lying at posterior end and along sides of body as far as acetabulum; ova few, relatively large. Dimensions of specimen in formalin, given in millimeters: Length, 2.72; breadth, anterior 0.43, at acetabulum 0.89, middle 1.07; near posterior 0.36; diameter of oral sucker, 0.26; diameter of acetabulum, 0.29; diameter of ovary, 0.21; diameter of testes, 0.33 and 0.39; ova, 0.11 and 0.07 in the two principal diameters."

The report of Stafford was criticized by Looss (1907) who deplored the naming of species which can not be recognized from their descriptions. He stated (p. 613), "Ich verweise als Beispiel hier auf einen neueren Artikel von Stafford (1904). In demselben wird eine ganze Anzahl von Gattungen und Arten neu benannt; unter ihnen finden sich solche, wie z. B. #14) *Xenodistomum melanocystis.*" After listing the diagnostic characters, Looss continued, "Es wird aber niemand behaupten können, dass mit der Veröffentlichung dem Leser auch nur ein leiser Fingerzeig über die wahre Natur des Genus und der Species gegeben ist. Die Namen sind leere Worte und trotzdem prioritätsrechtlich unantastbar." He added (p. 614), "Noch ein andres Beispiel: #32) '*Homalometron pallidum.* Stomach and duodenum of *Fundulus heteroclitus* L. (Killifish). New genus, new species . . . (Namenserklärung) . . . Linton, Bull. U. S. Fish Commiss. 1899. (1901) p. 422. Pl. 32. f. 354." Die zitierte Figur bei Linton, wenig Information gebend, wie leider die meisten dieses Autors, erinnert an ein *Allocreadium,* zeigt

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[1] This investigation was supported by Grant-NSF-G23561.

aber eine bestachelte Haut, würde also auf ein Mitglied der Gattung *Lepocreadium* Stoss. hinweisen."

Manter (1926) reported *Homalometron pallidum* in *Fundulus heteroclitus* from the coast of Maine. He noted the similarity to *Lepocreadium* and stated (p. 87), "So far as the description of Linton shows, the form could easily belong to this genus, the chief point of difference being the median location of the genital pore instead of a position to the left, as in *Lepocreadium*. The pore was clearly median in my material." But in addition to the difference in location of the genital pore, Manter noted that in *Lepocreadium* there is a prominent cirrus-sac which encloses the prostate gland and the anterior portion of a bipartite seminal vesicle, whereas in the species from *Fundulus* there is no cirrus-sac; the seminal vesicle is globular, not divided; and the duct from the vesicle is enclosed by glandular cells which lie free in the parenchyma. Moreover, the male duct is joined by the vagina to form a long, genital sinus. According to Manter, these features clearly distinguish *Homalometron* from *Lepocreadium* and *Homalometron* does not agree with the diagnosis of the subfamily Lepocreadiinae Odhner, 1905.

A timely and significant observation was made by Manter on the life-history of the species. He found encysted metacercariae in the stomach of *Fundulus* and very young worms, sometimes in large numbers, in the intestinal folds of the host. He concluded (p. 87) "As the Fundulus had been in salt water aquaria for some time, the indication is that infection is derived from marine rather than fresh water sources. In spite of the fact that immature specimens were sometimes found in large numbers, infection with the adult form was never heavy, and many uninfected fish were found. Usually not more than two or three specimens were taken from one host."

Looss (1894) described *Distomum isoporum* from the intestine of *Cyprinus carpio* and other fishes and he (1899) designated *D. isoporum* as type of a new genus, *Creadium*, and a new subfamily, Creadiinae. But the name *Creadium* was preoccupied and for it Looss (1900) substituted the name *Allocreadium*, whereby *ipso facto* the species, *isoporum*, remained type of the genus and subfamily. Looss (1902) named the subfamily Allocreadiinae and Stossich (1903) erected the family Allocreadiidae.

Meanwhile MacCallum (1895) described a distome from *Aplodinotus grunniens*, *Lepomis gibbosus*, and *Acipenser rubicundus* taken from Lake Erie and the Grand River of Ontario, as *Allocreadium* Looss var. *armatum*. Wallin (1909) described a new species, *Allocreadium lobatum*, with a history and revision of the genus *Allocreadium*. He noted that Looss (1902: 785) had pointed out that the species described by MacCallum is not a member of *Allocreadium*. However, Pearse (1924) identified specimens from *Aplodinotus grunniens* taken in Lake Pepin and Lake Michigan as *Allocreadium armatum* (MacCallum). Simer (1929) studied trematodes of fishes taken from the lower Tallahatchie River in Mississippi. In *A. grunniens* and *Polyodon spathula* he found the species described by MacCallum, common in smaller fishes and fewer in larger fishes. For it he erected a new genus, *Anallocreadium*. He stated that Looss had excluded the form from the Allocreadiinae; the absence of a cirrus-sac excludes it from the Lepocreadiinae; and the absence of oral papillae excludes it from the Stephanophialinae; but no final allocation was offered. Hunter and Bangham (1932) described *Anallocreadium* *pearsei* from *A. grunniens* and erected the subfamily Anallocreadiinae, which they included in the family Allocreadiidae. Manter (1936) erected the new genus, *Crassicutis*, and stated (p. 35), "The genera *Anallocreadium* and *Crassicutis* show affinities to the Lepocreadiinae through the genus *Homalometron*. . . . Further evidence of relationship to the Lepocreadiinae is to be sought in life history studies." Cable and Hunninen (1942) worked out the life-cycle of *Deropristis inflata* and discussed its systematic position. They showed that *Deropristis* can not be retained in the family Acanthocolpidae and that its nearest relatives are such forms as *Homalometron*, *Anallocreadium*, *Microcreadium*, and *Lepocreadium*. Accordingly, they accepted the Lepocreadiidae, a family erected by Nicoll[2] to contain the Lepocreadiinae Odhner and a group of similar and presumably related genera. In the family, Cable and Hunninen recognized three subfamilies: Lepocreadiinae Odhner, 1905; Deropristinae n. subfam.; and Homalometrinae (Anallocreadiinae Hunter and Bangham, 1932, renamed). In the Homalometrinae they included *Homalometron* Stafford, 1904; *Microcreadium* Simer, 1929; *Crassicustis* Manter, 1940; and an unnamed genus reported by Manter (1941). This genus was named *Opisthoporus* by Manter (1947) but the name was preoccupied and Manter (1949) replaced it with *Postporus*. Cable and Hunninen suppressed *Anallocreadium* Simer, 1929 as identical with *Homalometron* Stafford, 1904, a decision that was corroborated by Manter (1947) who added a new species, *Homalometron elongatum*, from *Gerres cinereus* taken in Florida. The description of the new species was supplemented by Bravo-Hollis and Manter (1957). G. C. Miller (1959) redescribed *Homalometron armatum* (MacCallum, 1895) and discussed the status of the genus; *Homalometron pearsei* (Hunter and Bangham, 1932) was suppressed as a synonym of *H. armatum*. The subfamily name was emended to Homalometroninae by Manter (1963a, p. 105).

A significant contribution to the life-cycle and taxonomy of the Homalometroninae was made by Hopkins (1937) who described and figured the cercariae of *Anallocreadium armatum* and *Microcreadium parvum*, two fresh-water species from the snail, *Amnicola peracuta*, taken in the Little Brazos River, Brazos County, Texas. The cercariae encysted in *Musculium ferrissi* and the older metacercariae resembled the adults so closely that tentative identification was possible. Hopkins stated (p. 94), "Both cercariae have: (1) cuticular spines, (2) setae or "sensitive hairs" covering the sides of the body, (3) three pairs of setae on the tail, (4) pigmented eyespots, (5) a long slender tail, and (6) no stylet. The second characteristic distinguishes them from the trichocercous cercariae of *Lepocreadium* and *Pharyngora*, the fifth distinguishes them from the microcercous or cotylocercous cercariae of *Plagioporous*, *Hamacreadium* and *Sphaerostoma*, and they differ from the ophthalmoxiphidiocercariae of *Allocreadium* and *Crepidostomum* in the first, second, third, and fifth characteristics. This new type of cercaria, which may be called the Anallocreadine type, may be defined as follows: Distome cercariae with straight slender tail, undivided sac-like excretory bladder, pigmented eyespots, cuticular spines, no stylet, numerous setae on sides of body, and three pairs of setae on tail; developing in rediae in freshwater snails."

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[2] The name Lepocreadiidae was first published in the Zoological Record for 1934, but the parts were issued separately and before the volume. Whether Part VI, which contains the literature on the Trematoda, was issued in 1934 or 1935 is uncertain.

MATERIAL AND METHODS

Anallocreadine cercariae were found emerging from *Hydrobia minuta* collected in the areas of Boothbay Harbor, Maine, and Woods Hole, Massachusetts. During the past six years, hundreds of *H. minuta* from the New England coast have been examined by isolation and crushing, and from 2% to 5% of the snails yielded the anallocreadine cercaria. Other trematode infections in *H. minuta* include an unidentified heterophyid, two unidentified microphallid species, and three species whose life-cycles have been worked out: *Levinsenilla minuta* Price, 1934 by Stunkard (1958); *Notocotylus minutus* n. sp., by Stunkard (1960a); and *Himasthla compacta* n. sp., by Stunkard (1960b).

The anallocreadine cercariae from *H. minuta* are very similar to those from *Amnicola peracuta* described by Sewell (1937) as larvae of *Anallocreadium armatum* [= *Homalometron armatum* (MacCallum, 1895) Manter, 1947]. These cercariae are produced in rediae in *H. minuta* and emerge principally at night. They are photonegative and accumulate on the dark side of a finger-bowl. They swim tail first, with the body contracted and bent ventrally until it appears almost spherical, and the tail extended and lashing vigorously. This action of the tail lifts the larva in the water and pulls it along. The cercariae creep by alternate attachment of the oral and ventral suckers, and under a cover-glass the body, which is almost cylindrical, often rolls over as it moves. The acetabulum is protrusible and in lateral view may appear almost stalked. Alive and stained with neutral red or Nile blue sulphate, the internal structures, other than the excretory tubules and flame-cells, are often conspicuous.

These cercariae were left in finger-bowls with various invertebrates from the area where the snails were collected. They penetrated and encysted in *Gemma gemma,* uninfected *H. minuta,* and small polychaete annelids. Attempts to infect various crustaceans and small fishes gave only negative results. Laboratory-infected *G. gemma* were fed to *Fundulus heteroclitus* that had been held in the laboratory for three to four weeks and very small, recently excysted, worms were recovered, identical with those of natural infections. Moreover, a series of specimens, from juveniles to mature, gravid *H. pallidum* were taken from natural infections of *F. heteroclitus.* The youngest worms were recently excysted metacercariae and the gravid worms each contained a few, 3 to 15, large, unembryonated eggs. Some of these eggs were incubated in sea water and later fed to laboratory-raised *H. minuta.* Six weeks later, these snails were liberating cercariae, identical with those of natural infections. The production of experimental infections in both snails and fishes establishes the life-cycle of the parasite. All stages were studied alive and after fixation and staining. Serial sections of infected snails gave details of the asexual generations, but sporocysts were not observed.

STAGES IN THE LIFE-CYCLE

Adult

Sexually mature worms have been described by Linton (1901; fig. 354); Stafford (1904); Manter (1926; figs. 54, 55, 56); and M. J. Miller (1941; fig. 2) who restudied the specimens in the Stafford collection. Linton's figure of the type specimen is reproduced (Fig. 1). Manter (1931) listed *Distomum globiporum*

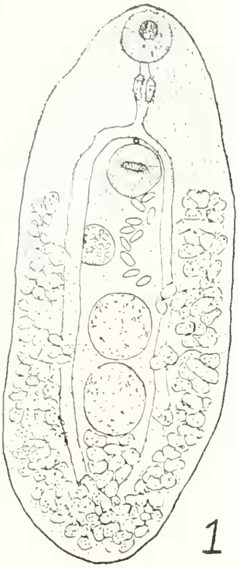
Rudolphi of Linton, 1905 from *Fundulus majalis* and *Leistomus xanthurus* and the worms designated as (*Lepocreadium*) *serospinosum* sp. inq. of Nicoll, 1909, as synonyms of *Homalometron pallidum*. As additional hosts, Linton (1940) listed *Menticirrhus saxatilis, Morone americana, Pseudopleuronectes americanus, Tautoga onitis* and *Bairdiella chrysura*. It is probable that specimens from some of these hosts have not been identified correctly, and there is the further possibility that worms taken from the intestine of predatory fishes may have been ingested with prey. In the present study, the largest specimen without eggs measures 1.12 mm. in length and is shown in Figure 3. Ovigerous worms measure from 0.80 to 2.80 mm. in length. The eggs are few, 3 to 15; 0.10 to 0.11 mm. in length and 0.06 to 0.07 mm. in breadth. They are not embryonated when passed.

Metacercaria

On encystment, the worms are bent ventrally so that the ends tend to approach each other and the suckers may appear almost opposite one another. The ocelli usually are situated near one end of the cyst (Fig. 6). The cysts are oval, 0.08 to 0.10 mm. in length and 0.075 to 0.808 mm. in width. The wall is very thin and excystment is easily accomplished. A recently encysted worm, released and pressed to study the excretory system and then fixed, is 0.24 mm. long and 0.11 mm. wide; the oral sucker is 0.048 mm. in diameter and the acetabulum, much flattened, is 0.056 mm. in diameter. A much older specimen of natural infection, released and measured without pressure, was 0.26 to 0.30 mm. long and 0.13 to 0.20 mm. wide; the oral sucker was 0.057 to 0.064 mm., the acetabulum 0.062 to 0.064 mm., and the pharynx 0.024 to 0.026 mm. in diameter. In this specimen the pigment of the eye-spots was becoming diffuse and scattered. These measurements show that there is little development or growth in the second intermediate host.

Redia

In this species, as in many digenetic trematodes, each redia produces one or more daughter rediae before the formation of cercarial embryos. The rediae are oval, to pyriform, to elongate, with a pointed posterior end. The body wall is composed of circular, longitudinal and oblique muscles, and although there are no foot-like protrusions, the smaller rediae are very mobile. As they fill with cercariae, the ability to change shape is restricted. Figure 5 shows a mother and daughter redia of experimental infection. The mother is 0.240 mm. long, 0.176 mm. wide, and the pharynx is 0.052 mm. in diameter. The daughter redia is 0.126 mm. long, 0.032 mm. wide and the pharynx is 0.026 mm. in diameter. The cercarial embryo is 0.148 mm. long and 0.074 mm. wide. Figure 4 shows a daughter redia of average size. It is 0.375 mm. long, 0.125 mm. wide, and the pharynx is 0.055 mm. in diameter. Larger rediae measure up to 0.72 mm. in length, 0.22 mm. in width and with pharynges from 0.057 to 0.065 mm. in diameter. The pharynx is protrusible and retractile; when retracted there is a distinct oral funnel. In small rediae the intestine extends one-half or more of the length of the body, but it does not increase as the redia enlarges and is more and more restricted to the anterior end of the body. It contains yellow droplets and amorphous blackish material, the residue of ingested snail tissue. The excretory system is double; there are



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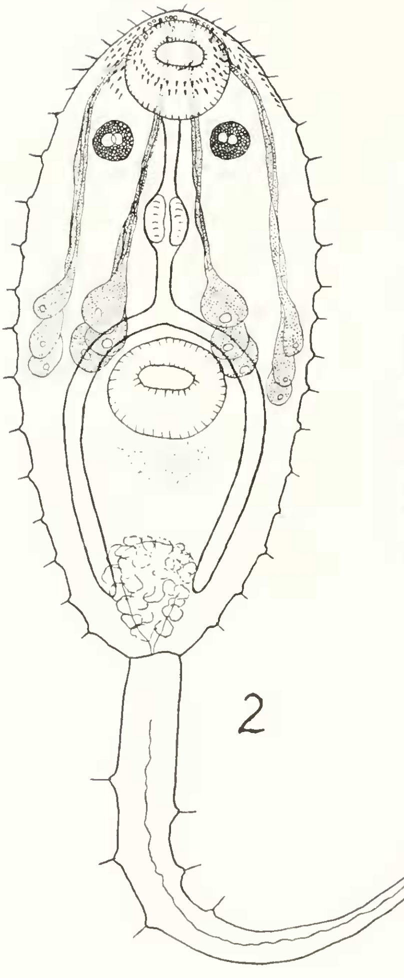

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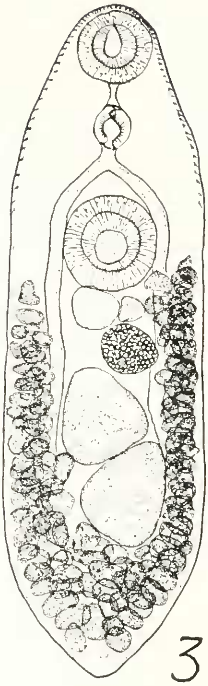

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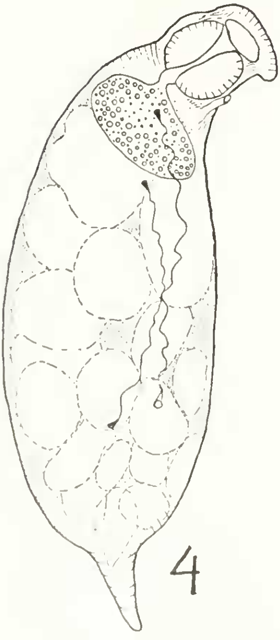

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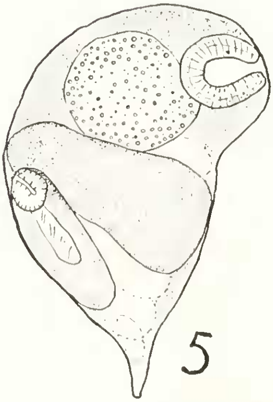

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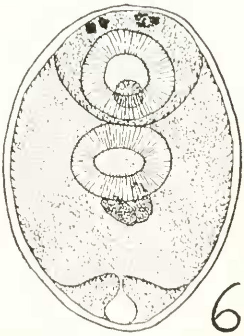

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excretory pores on either side of the body, about one-third of the body length from the posterior end. From each pore, a tubule extends forward past the middle of the body where it divides; a recurrent branch passes backward past the excretory pore and terminates in a flame-cell; the anterior branch soon divides and each branch ends in a flame-cell as shown in Figure 4. The birth-pore is ventral, at the level of the posterior edge of the pharynx, and when the redia is pressed its contents may be extruded through the pore. The snail is very small, the cercariae are relatively large, and are produced in small numbers.

Cercaria

The cercariae were studied alive and after fixation and staining. Live study is far more rewarding, especially when vital dyes, neutral red and Nile blue sulphate, are employed. Stained lightly with neutral red, the granules in the cells that form the wall of the excretory bladder stain a brick red; the contents of the intestine form spherules of deep dark red; the penetration glands stain a lighter red and the cells of the germinal complex take a light lilac color. The body is oval to elongate; it measures 0.14 to 0.325 mm. in length and 0.08 to 0.135 mm. in width. Under pressure of a cover glass the apparent size of the larva and its organs increases and the body may measure 0.50 by 0.18 mm. The tail is slightly subterminal; retracted, it is much shorter than the body and since body and tail are ordinarily not extended at the same time, when the tail is extended it is longer than the body. It varies from 0.095 to 0.230 mm. in length and the tip is papilliform. The body has lateral papillae, each of which bears a seta, but the setae are easily lost. The tail has three pairs of lateral papillae with setae 0.008 to 0.009 mm. long. They are situated near the middle of the tail; also there is a low dorsoventral fin-fold, that is somewhat wider distally. The acetabulum is slightly posterior to the middle of the body, the same size as the oral sucker, and measures 0.05 to 0.06 mm. in diameter. The cuticula is spined, the spination more conspicuous anteriorly and diminishing posteriorly, where in young cercariae it can be seen only with oil immersion magnification. There is a pair of ocelli, equipped with lenses, situated directly above the transverse commissure of the nervous system and anterior to the pharynx. There are twelve to fifteen granules, each about one micron in diameter in any diameter of the ocellus; the ocelli measure 0.016 to 0.020 mm. in diameter. The mouth is subterminal, the oral sucker is 0.050 to 0.060 mm. in diameter. The prepharynx is longer than the esophagus and the pharynx, 0.02 to 0.024 mm. in diameter, is immediately posterior to the level of the ocelli, with the

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EXPLANATION OF PLATE

All figures are of *H. pallidum*

FIGURE 1. Type specimen, after Linton, 1901; ventral view.

FIGURE 2. Cercaria, from *Hydrobia minuta*, drawn from sketches made during study of living specimens.

FIGURE 3. Largest non-gravid specimen from intestine of *Fundulus heteroclitus*, natural infection; dorsal view.

FIGURE 4. Daughter redia, from natural infection of *H. minuta*.

FIGURE 5. Mother redia, with daughter and first cercarial larva; experimental infection of *H. minuta*.

FIGURE 6. Encysted metacercaria, from *Gemma gemma;* experimental infection.

anterior edge of the pharynx at the level of the posterior edge of the ocelli. The digestive tract bifurcates a short distance anterior to the acetabulum. The ceca are long, ending blindly at the sides of the excretory vesicle. There are six pairs of penetration glands on each side of the body, situated anterior and lateral to the acetabulum. The ducts of three gland cells pass forward on the median side of the ocellus and the ducts of the other three glands pass lateral to the ocellus. All open at the anterior end of the body, above the mouth. The excretory vesicle is saccate, its wall formed by a large number of glandular cells which stain intensely with vital dyes. From the anterolateral sides of the vesicle, collecting ducts pass forward to the level of the acetabulum where they divide into anterior and posterior branches. Each branch bears three groups of flame-cells and although the pattern has not been completely worked out, it appears to be $(3 + 3 + 3) + (3 + 3 + 3)$.

SYSTEMATIC RELATIONS

The morphology of the sexually mature worms and of the successive larval stages of *H. pallidum* supports the proposal of Cable and Hunninen (1942) that the genus *Homalometron* is a member of the family Lepocreadiidae. Despite the accrual of much information on the morphology, life-cycles, larval stages and bionomics of the lepocreadiid trematodes, there is much difference of opinion concerning their systematic relations. The subfamilies Lepocreadiinae and Homalometrinae were included by Yamaguti (1958) in the family Allocreadiidae. The family as conceived contained 25 subfamilies and includes such diverse and disparate types that inherent unity is lacking. Indeed, in a footnote the author predicated (p. 95), "This family name is used tentatively in a broad sense."

On the basis of life-history studies, Cable and Hunninen (1942) removed *Deropristis* from the family Acanthocolpidae and included it in the Lepocreadiidae. Subsequent authors, Dawes (1946), Skrjabin (1954), Bykhovskii and Dubinina (1954), and Yamaguti (1958) retained *Deropristis* in the Acanthocolpidae but Skrjabin (1958) removed the Deropristinae from the Acanthocolpidae and elevated the subfamily, which contained also *Skrjabinopsolus* Ivanov and Murygin, 1937 (syn. *Pristotrema* Cable, 1952) and *Pristicola* Cable, 1952, to family rank. Peters (1961) accepted the family Deropristiidae which he emended to include two subfamilies: Deropristiinae Cable and Hunninen, 1942 and Cestrahelminae n. subfam., erected to contain *Cestrahelmins* Fischthal, 1957, described originally as a genus of "uncertain familial relationships." The action of Peters was approved by Fischthal and Kuntz (1963) but Baer and Joyeux (1961) retained the Deropristinae as a subfamily in the Lepocreadiidae.

Present concepts concerning the limits and composition of the Lepocreadiidae derive in large part from the studies of Cable and Manter. In a series of papers, Manter has reported on the morphology, distribution-patterns, zoogeographical affinities and taxonomy of the trematode parasites of marine and fresh-water fishes. He (1933) erected a new genus, *Eurypera*, to contain *Distomum gyrinus* Linton, 1907 and other species, and a new family Euryperidae. Since the generic name was preoccupied, Manter (1934) renamed the genus, *Megapera*, and the family Megaperidae. Cable (1954) worked out the life-cycle of *M. gyrina* and noted the similarity of its cercaria to the trichocercous larvae of the Lepocreadiidae. He postulated close relationship between the Megaperidae and Lepocreadiidae. Manter

(1963a) compared morphological features of the two families and stated (p. 99), "Megaperidae Manter, 1934 is reduced to a subfamily, Megaperinae, of the Lepocreadiidae." He observed (p. 105), "The derivation of the generic name *Homalometron* Stafford, 1904, requires Homalometroninae rather than "Homalometrinae." Dollfus (1950) erected a new genus, *Trematobrien,* and a new family, Trematobrienidae, to contain a species, *Trematobrien haplochromios,* from *Haplochromis moffati* of the Belgian Congo. Manter (1962) noted the resemblance of *Trematobrien* and *Crassicutis* Manter, 1936 and borrowed the type specimens of *T. haplochromios.* Study of this material led to the suppression of Trematobrienidae and the inclusion of *Trematobrien* in the subfamily Homalometroninae of the Lepocreadiidae.

In a survey of the family, Manter (1963b) stated that the lepocreadiids are almost entirely parasites of marine fishes, and that the subfamily Homalometroninae is of particular significance since its members occur in marine, brackish, and a few fresh-water fishes. He discussed the geographical dispersal of the subfamily and the possible significance of present distribution for the phylogeny and evolution of the hosts and their parasites. Relating hostal and geographical relations, Manter observed that *Crassicutis* Manter, 1936 occurs in cichlid fishes of Yucatan and the related genus, *Trematobrien* Dollfus, 1950 is in cichlids of the Congo. These are tropical fresh-water fishes of South and Central America and the West Indies and of Africa, Syria, Madagascar and South India. Many can live in brackish water, which suggests a coastal connection between the continents involved. *Crassicutis* has two marine species in the Gulf of Mexico and two species in Lake Valencia, Venezuela. The genus, *Microcreadium* Simer, 1929, is in the fresh-water drum, *Aplodinotus,* which belongs to a predominantly marine family. North of the tropics, the subfamily is represented by the genus *Homalometron* whose species occur in marine, brackish and a few fresh-water fishes. Manter concluded (p. 59), "In general, the subfamily illustrates an evolution from marine ancestors, through secondary-division hosts, to become parasites of freshwater fishes." The idea of host-specificity and parallel evolution in parasitic flatworms is not new. It was discused by Stunkard (1957) who maintained (p. 261), "Present information indicates that the adoption of the parasitic habit occurred at an extremely remote period and that the evolution of parasitic life-cycles, with accompanying adaptations of parasites, has proceeded hand in hand with the evolution of their hosts. The presence of closely related trematodes in marine and freshwater hosts may be explained on the assumption that the primitive hosts harbored the ancestors of present species and that the hosts separated and differentiated into marine and fresh-water types."

SUMMARY

The successive stages in the life-history of *Homalometron pallidum,* a parasite of *Fundulus heteroclitus,* described by Linton, 1901 and named by Stafford, 1904, have been discovered and identified. The asexual generations are in *Hydrobia minuta* and the metacercarial stages are encysted in *Gemma gemma, H. minuta,* and small polychaete annelids which serve as secondary intermediate and transfer hosts. Knowledge of larval as well as adult stages gives a better basis for determination of the evolution and systematics of the allocreadiid-leprocreadiid trematodes. The subfamily Homalometroninae contains marine, brackish-, and fresh-

water species. Manter (1963) discussed the geographical dispersal of the group and the possible significance of present distribution for the phylogeny and evolution of the parasites and of their hosts. In his opinion, the subfamily illustrates an evolution from marine ancestors, through secondary-division hosts, to become parasites of fresh-water fishes. Results of the present investigation support his hypothesis.

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